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10.—Notes on the Skulls of two Western Australian Rodents with a key to the Skulls of the Rodents of Southwestern Australia

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Remains of two species of Western Australian rodents, *Pseudomys (Gyomys) occidentalis* and *Pseudomys (Pseudomys) rawlinnae*, hitherto known from small samples and few localities have been found in several caves along the west coast of Australia and along the south edge of the Nullarbor Plain. *Pseudomys (Gyomys) occidentalis* is reported for the first time from the southern Nullarbor Plain. Minor morphological differences can be seen in samples from different areas.

Pseudomys (Pseudomys) rawlinnae is shown to vary in the presence of an accessory cusp on the anterior edge of M^1, the degree of interorbital constriction and the degree of development of the spine on the zygomatic plate. This variation makes it difficult to distinguish this species from *Pseudomys (Thetomys) nanus* on the basis of fragmentary material.

Statistical tables on each species and a key to the skulls of the rodents of southwestern Australia are given.

Introduction

Investigations of cave sediments from Western Australia have resulted in the collection of abundant material of two species of rodents, *Pseudomys (Gyomys) occidentalis and Pseudomys (Pseudomys) rawlinnae*, which have previously been known only from sparse material.

The author (Lundelius 1957, 1960, 1963) has previously reported the presence of these two species in cave deposits in Western Australia but no details concerning their morphology were given. The samples which form the basis of this report are large enough to give reliable estimates of the variability of some cranial and dental characters. This should facilitate comparisons with samples from other areas as they are found.

The present samples are obtained from the following caves: Murraelellevan, 32° 2′S. 126° 4′E.; Madura, 32° 0′S. 127° 0′E.; Webb and Snake Pit, 31° 46′S. 127° 51′E.; and Abrakurrie, 31° 39′S. 128° 26′E.

Pseudomys (Pseudomys) rawlinnae

This species was named by Troughton (1932) on the basis of material from the vicinity of Rawlinna, Western Australia. Finlayson (1939) described a series from the vicinity of Ooldea, South Australia and gave the range and mean of the measurements of four males and four females. All of the material considered here comes from caves along the Eyre Highway between Balladonia and Eucla.

The largest sample and the one which forms the basis of the statistical data, comes from Murraelellevan Cave. Smaller samples are available from Madura, Webb, Snake Pit and Abrakurrie caves. Except for the material from Madura and Abrakurrie caves which contain some fill, all the specimens were collected from the surface where they were associated with remains of the rabbit *Oryctolagus cuniculus* and the house mouse *Mus musculus*. These two species have been introduced by the European colonists within the last century. While there is always the possibility of the remains of the introduced species being mixed with older material, the condition and the thorough mixing of the bones indicates that all the surface material is essentially the same age. The presence of well-preserved bones of only small animals indicates that owls were responsible for the bone deposits.

The skull of this species closely resembles that of *Pseudomys shortridgei* but is smaller and more lightly built. The anterior edge of the zygomatic plate is gently concave as in *Pseudomys shortridgei*, but there is more of a tendency to develop a dorsal spine. Some specimens have a well developed spine, others have the dorsal border of the zygomatic plate angled but with no spine. Although members of the genus *Notomys* also have the spine they are easily distinguished by the broadening of the upper surface of the anterior part of the zygoma. There is no broadening in *Pseudomys rawlinnae*.

The skull shows considerable variation in the width and shape of the interorbital area (Fig. 1). The width of the zygomatic arches also appears to be variable but an objective measurement is difficult on the present material. Some of this variation in the skull is probably attributable to age differences. Two skulls (CNHM PM-4294, PM4352) which show narrow zygomatic width, shortened rostra and rounded skulls have unworn teeth indicating that they are from relatively young individuals. Sexual differences may also be involved but no data are available on sexual dimorphism.

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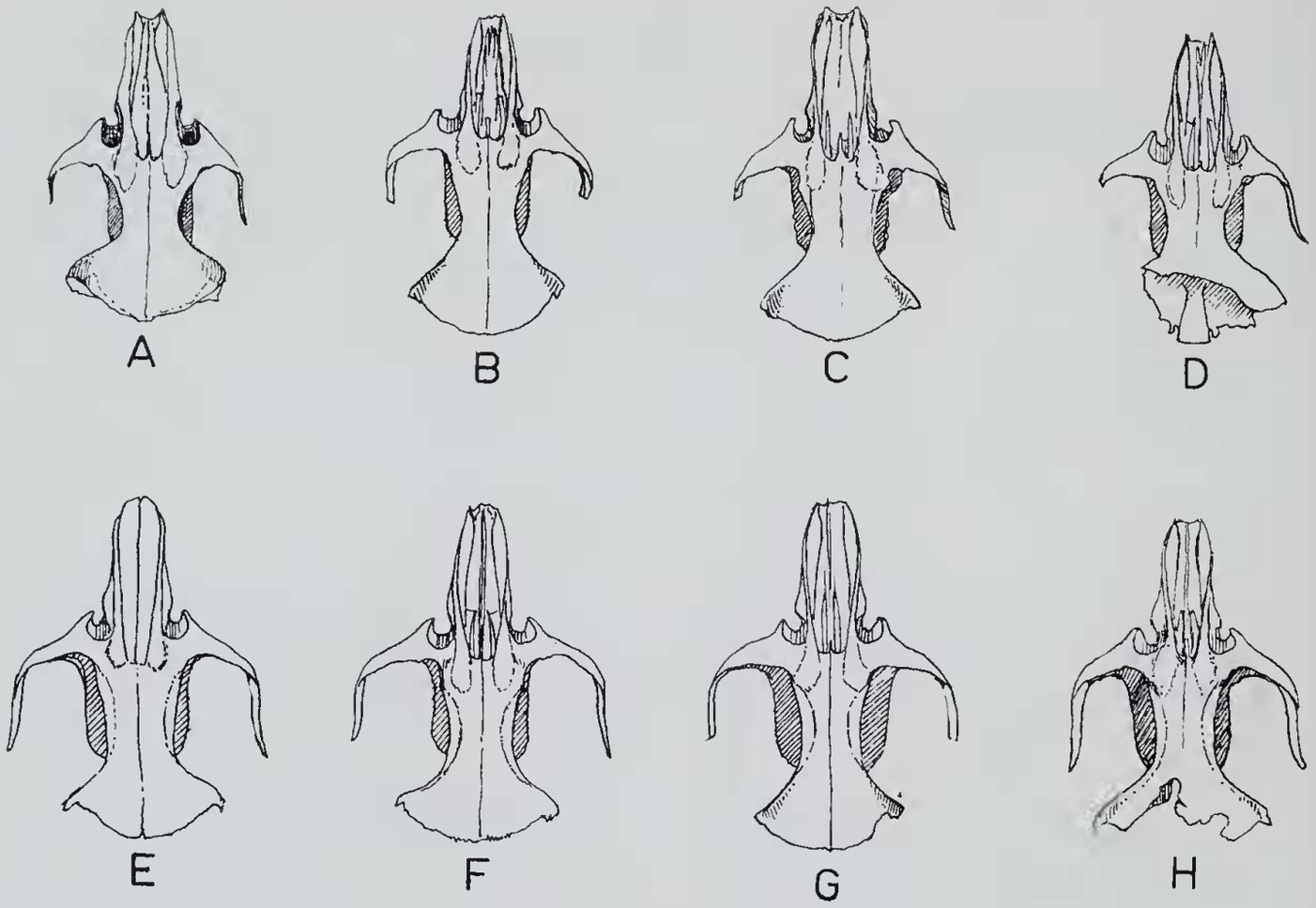

Fig. 1.—Dorsal views of eight skulls of *Pseudomys (Pseudomys) rawlinnae* from Murraelellevan Cave showing variation in interorbital region. x2. A—PM 4294; B—PM 4357; C—PM 4295; D—PM 4296; E—PM 4339; F—PM 4344; G—PM 4349; H—PM 4347.

TABLE 1

Statistical Data for a Sample of *Pseudomys (Pseudomys) rawlinnae* from Murraelellevan Cave and a Sample from Ooldea, South Australia.

	Sample from Murraelellevan Cave					Sample from Ooldea*			
						4 Males		4 Females	
	No.	Mean	Standard Deviation	Coefficient of Variation	Observed Range	Mean	Observed Range	Mean	Observed Range
Total length upper molars	38	4·95±·03	·23	4·6	4·64–5·48	5·1	5·0–5·2	5·2	5·0–5·3
Length M^1	38	2·42±·01	·097	4·0	2·23–2·65	....	....	....	....
Length M^2	37	1·43±·01	·11	7·4	1·30–1·76	....	....	....	....
Length M^3	38	1·15±·01	·084	7·4	·97–1·29	....	....	....	....
Width M^1	38	1·66±·01	·079	4·7	1·53–1·79	....	....	....	....
Interorbital width	22	3·88±·04	·208	5·36	3·49–4·19	4·0	3·9–4·1	4·1	3·9–4·5
Nasal length	3	10·82	....	....	10·43–11·45	11·5	11·3–11·7	11·2	11·0–11·6
Palatal length	29	13·28±·11	·608	4·58	12·21–14·55	15·6	15·1–16·3	16·0	15·6–16·6
Length anterior palatal foramina	29	6·17±·09	·504	8·17	5·05–7·03	6·6	6·6–6·6	6·8	6·7–6·9
Alveolar length upper molars	39	5·40±·04	·287	5·31	5·02–6·17	....	....	....	....

* Data from Finlayson (1939.)

The teeth are similar to those of *Pseudomys shortridgei* but, as in the case of the skull, they are smaller (Tables 1 and 2). The laminæ of the upper teeth do not slope as much as in *Pseudomys shortridgei*. The teeth show some variation in the degree of development of the external row of cusps, presence of an accessory cusp on the anterior edge of M^1 and the number of posterior cusps of M^3 and their configuration. Of 89 specimens from Murrælellevan Cave, 18 (or 20%) possess a well defined accessory cuspule on the anterior edge of M^1. A statistical comparison of samples with the cuspule and without it, shows no difference in the length of M^1. Of 79 right M^3's from Murraelellevan Cave, 75 have a single posterior cusp free of the midloph, 2 have it connected to the midloph and 2 have two free posterior cusps.

TABLE 2

Statistical Data on a Sample of Pseudomys (Pseudomys) shortridgei from the Top One Foot of Sediments, Hasting's Cave, Western Australia.

	No.	Mean	Standard Deviation	Coefficient Variation	Observed Range
Total Length Upper Molars	25	5·76 ± ·054	·27	4·70	5·23–6·11
Length M^1	34	2·68 ± ·030	·18	6·54	2·32–2·91
Length M^2	26	1·70 ± ·023	·12	6·99	1·45–1·91
Length M^3	25	1·35 ± ·021	·11	7·93	1·15–1·57
Width M^1	34	1·91 ± ·018	·11	5·58	1·76–2·07

An examination of the coefficients of variation given in Table 1 reveals that they are all within the range to be expected in a population of mammals. This implies that either this population does not exhibit the high variability said to be characteristic of some Australian desert species (Jones 1923) or the sample from Murraelellevan Cave was accumulated in a very short period of time.

A comparison of the Murraelellevan Cave material with Finlayson's figures shows the two samples to be similar. However, a comparison of measurements of five characters of Finlayson's Ooldea sample with the Murraelellevan Cave sample shows that the former measurements always average larger. In two characters, nasal length and palatal length, no specimen from Murraelellevan Cave is as large as the largest Ooldea specimen (Table 1). These minor differences probably do not have much significance. Both samples are small so far as some characters are concerned and may not be representative of either population. It is to be expected that different populations of a species will show small differences.

The mandibles and lower dentitions are so similar to those of *Notomys mitchelli*, which occurs in the same area, that differentiation is extremely difficult and no attempt is made to describe them here.

The skull of *Pseudomys rawlinnae*, despite its general resemblance to that of *Pseudomys shortridgei*, is readily distinguished by its generally smaller size, lighter build and better developed anterior spine on the zygomatic plate. There seems to be no reason for not regarding them as good species until such time as morphologic intergrades are found.

Pseudomys rawlinnae is far more likely to be confused with *Pseudomys nanus*. Both species have a spine on the zygomatic plate, no broadening of the upper anterior surface of the zygoma and, as noted above, some specimens of *Pseudomys rawlinnae* have an accessory caspule on the anterior edge of M^1 as in *Pseudomys nanus*.

Figures 2, 3 are scatter diagrams of width of M^1 against length of M^1 and length of M^3 against length of M^3 showing the relationships between a Recent sample of *Pseudomys nanus*, 2 subfossil samples of *Pseudomys nanus* and a sample of *Pseudomys rawlinnae*. It is clear that the principal difference between *Pseudomys nanus* and *Pseudomys rawlinnae*. is size. This is of little help in deciding whether they might be conspecific since size is frequently different

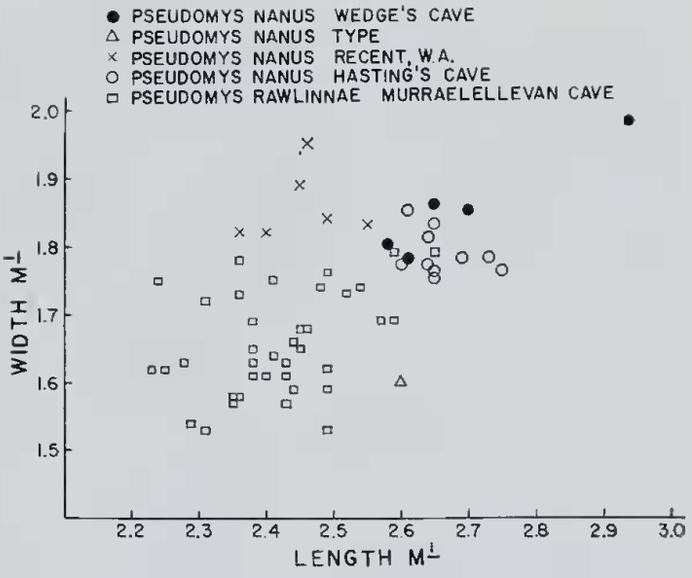

Fig. 2.—Scatter diagram showing relationship between length of M^1 and width of M^1 in several samples of *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys rawlinnae* from Western Australia.

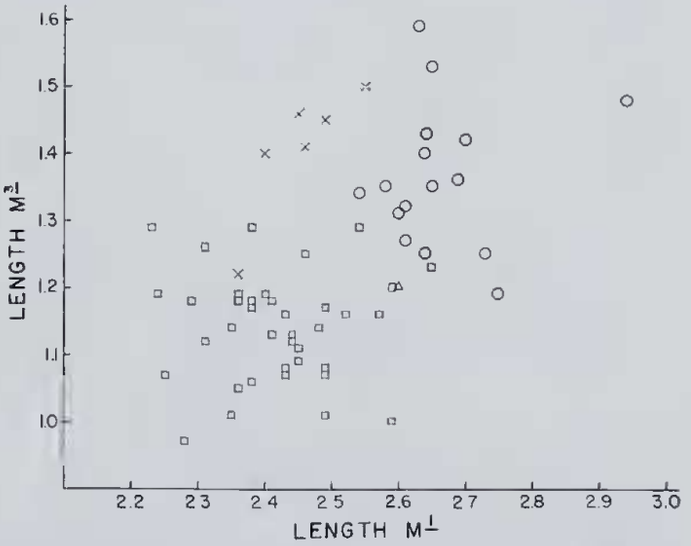

Fig. 3.—Scatter diagram showing relationship of length of M^1 and length of M^3 in several samples of *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys) rawlinnae* from Western Australia. See figure 2 for explanation.

in different populations of the same species. It is also interesting that the subfossil samples of *Pseudomys nanus* seem to show a slightly larger size than the Recent sample.

Although the type locality of *Pseudomys nanus* is along the west coast of Western Australia, a large part of the intervening area is essentially the same as the known area of occurrence of *Pseudomys rawlinnae* and it is quite possible that it actually occurs over a wide area. Finlayson (1941) has recorded a rodent which he refers to *Pseudomys nanus* from 10 miles south of Koonapandi in Central Australia. The presence of very similar rodents in widely scattered localities in central and western Australia suggests that they might be local populations of one widely distributed species.

Pseudomys (Gyomys) occidentalis

Pseudomys (Gyomys) occidentalis was described by Tate (1951) from two specimens from Tambellup, southwestern Australia. Until the

material from the caves in western Australia was discovered these were the only known specimens.

The material described here comes from caves along the west coast of Australia and from the Nullarbor Plain (Lundelius 1957, 1960, 1963). This new material not only adds to the known geographic range of the species but also shows that the species varies morphologically over its range.

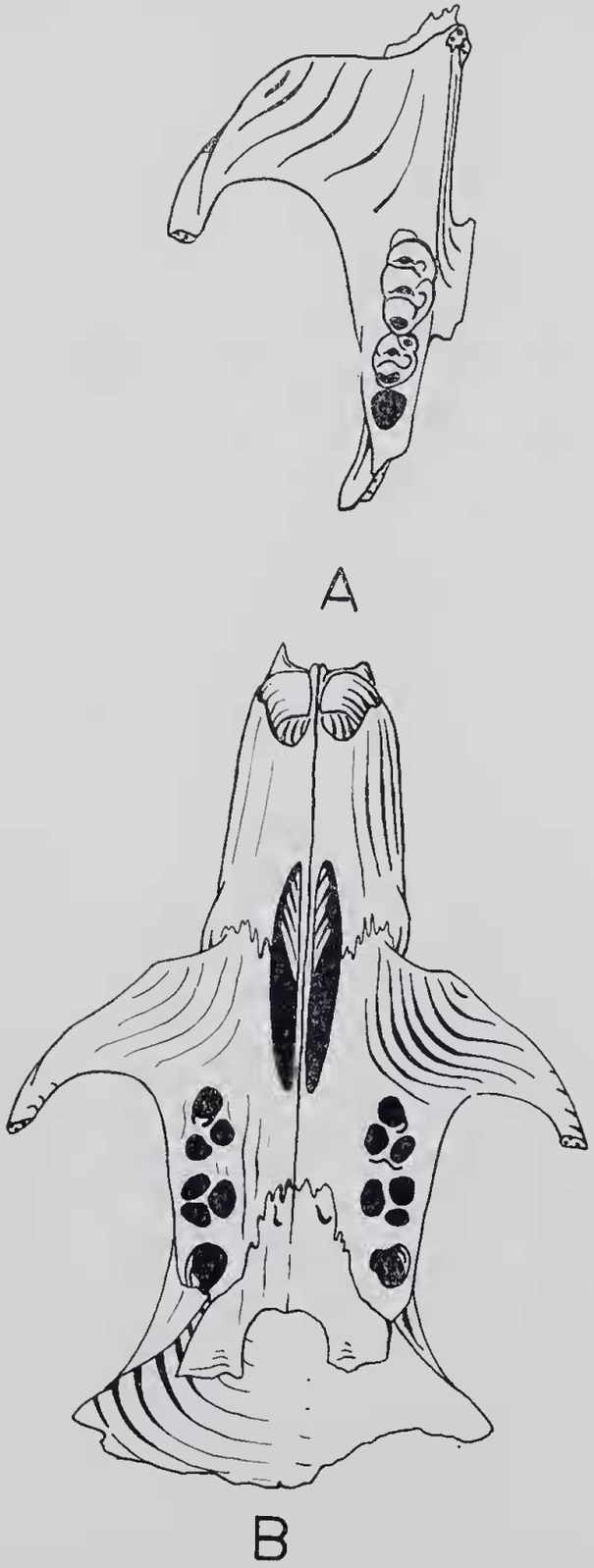

Fig. 4.—Ventral view of maxillary (A) and palate (B) of *Pseudomys (Gyomys) occidentalis* from Murraelellevan Cave. x 5.

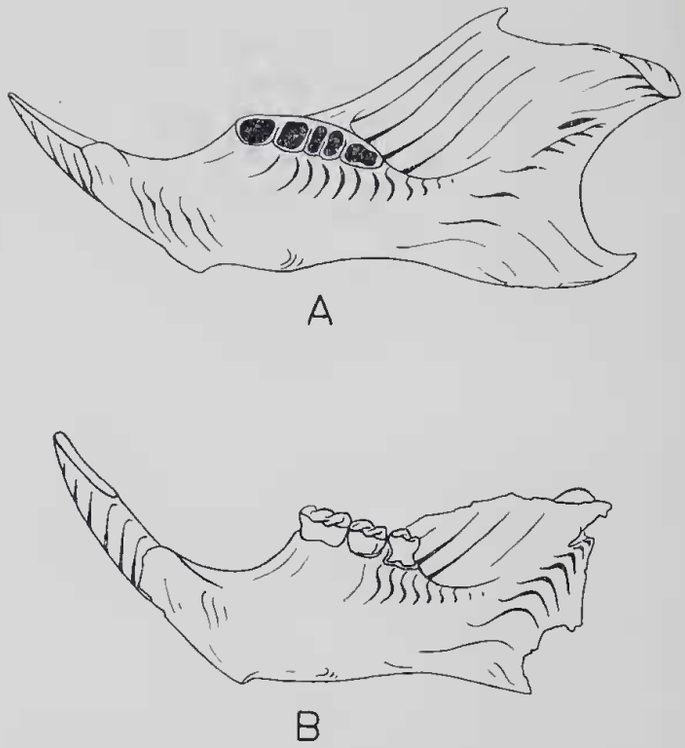

Fig. 5.—Lingual view of mandible of *Pseudomys (Gyomys) occidentalis* from Murraelellevan Cave. x 4.

The presence of *Pseudomys (Gyomys) occidentalis* in the Recent deposits at Jurien Bay reported by the author (Lundelius 1957) extended its known range 300 miles northward and indicated a wide distribution in the semi-arid portions of western Australia. The discovery of remains of this species in surficial deposits of Murraelellevan Cave on the Nullarbor Plains extends its range 500 miles eastward into a very dry area and indicates that the species had in the very recent past a very wide distribution in the southern part of western Australia.

The skull of this species is characterized by a broad zygomatic plate with a straight anterior edge and no spine at the top. The anterior part of the zygomatic arch is not broadened. The molars, both upper and lower, are very small in proportion to the size of the skull, very short crowned and have almost no inclination to the laminæ. No specimens have been seen with an accessory cuspule on the anterior edge of M^1.

Table 3 gives measurements for the type and paratype, several specimens from Murraelellevan Cave and statistical data on a sample from Hasting's Cave near Jurien Bay. It can be seen that there are few significant differences between these three widely separated samples. The greatest difference is the generally smaller size of the Nullarbor sample. Although the sample is small it consistently falls slightly below or in the lower end of the observed range of the Hasting's Cave sample.

The differences between the Hasting's Cave sample and the type and paratype from Tambellup are much smaller. The length of the lower molars, M_1, M_2, width of M_1, length of M^1, M^2 and width of M^1 of the Tambellup specimens are either slightly above or at the upper end of the observed range of the Hasting's Cave sample.

TABLE 3

Statistical Data on a Sample of *Pseudomys (Gyomys) occidentalis* from the Surface Layer of Hasting's Cave and Murraelellevan Cave, Western Australia, compared with the Type and Paratype

	Hasting's Cave Sample				Recent Western Australian		Murraelellevan Cave Sample		
	No.	Mean	Standard Deviation	Coefficient Variation	Observed Range	CNHM 34725 Type	CNHM 34726	No.	Mean	Observed Range
Length M^1	10	1·96 ± ·038	·12	6·28	1·78–2·14	2·09	2·11	....	....	....
Length M^2	15	1·36 ± ·01	·04	2·85	1·27–1·41	1·30	1·39	....	....	....
Length M^3	9	1·02 ± ·03	·09	8·70	·88–1·15	·95	·98	....	....	....
Width M^1	10	1·34 ± ·009	·03	2·24	1·28–1·44	1·37	1·47	....	....	....
Width across M^1's (alveolar)	12	5·20 ± ·052	·18	3·42	4·84–5·50	....	....	....	....	....
Width between M^1's (alveolar)	15	2·78 ± ·049	·19	6·82	2·22–2·99	....	....	....	....	....
Width across M^3's (alveolar)	5	5·11	·21	4·15	4·84–5·32	....	....	....	....	....
Width between M^3's (alveolar)	11	3·34 ± ·081	·27	8·02	2·92–3·80	....	....	....	....	....
Width across ant. end premaxilla	16	2·75 ± ·065	·26	9·43	2·42–3·30	2·34	2·56	....	....	....
Upper alveolar length	26	4·71 ± ·056	·29	6·19	4·26–5·82	4·44	4·46	2	4·30	4·26–4·34
Length post incisor diastema	21	7·66 ± ·091	·42	5·44	7·00–8·44	7·62	7·91	....	....	....
Interorbital width	8	4·13 ± ·17	·50	12·19	3·68–5·23	4·04	4·32	....	....	....
Depth of rostrum at tubercle	15	6·99 ± ·098	·38	5·43	6·08–7·45	6·18	6·57	....	....	....
Length incisive foramina	16	4·96 ± ·065	·26	5·26	4·61–5·47	5·1*	5·6*	....	....	....
Length lower molars	13	4·53 ± ·022	·08	1·78	4·38–4·68	4·58	4·67	....	....	....
Length M_1	20	2·01 ± ·013	·06	3·13	1·85–2·12	2·13	2·10	3	1·92	1·83–1·99
Length M_2	14	1·35 ± ·008	·03	2·52	1·30–1·41	1·37	1·46	....	....	....
Length M_3	14	1·10 ± ·018	·07	6·72	·97–1·23	·99	1·07	....	....	....
Width M_1	20	1·19 ± ·009	·04	3·30	1·13–1·29	1·23	1·30	3	1·17	1·16–1·19
Length lower post incisor diastema	19	4·30 ± ·066	·29	6·65	3·73–4·91	3·82	4·10	4	3·93	3·56–4·49
Alveolar length lower molars	20	4·60 ± ·029	·13	2·80	4·39–4·86	4·62	4·58	4	4·54	4·15–5·42
Depth of jaw at center M_1	18	4·12 ± ·059	·25	5·98	3·55–4·50	3·78	4·00	4	3·29	2·98–3·61

* Measurements from Tate (1951); CNHM, Chicago National History Museum.

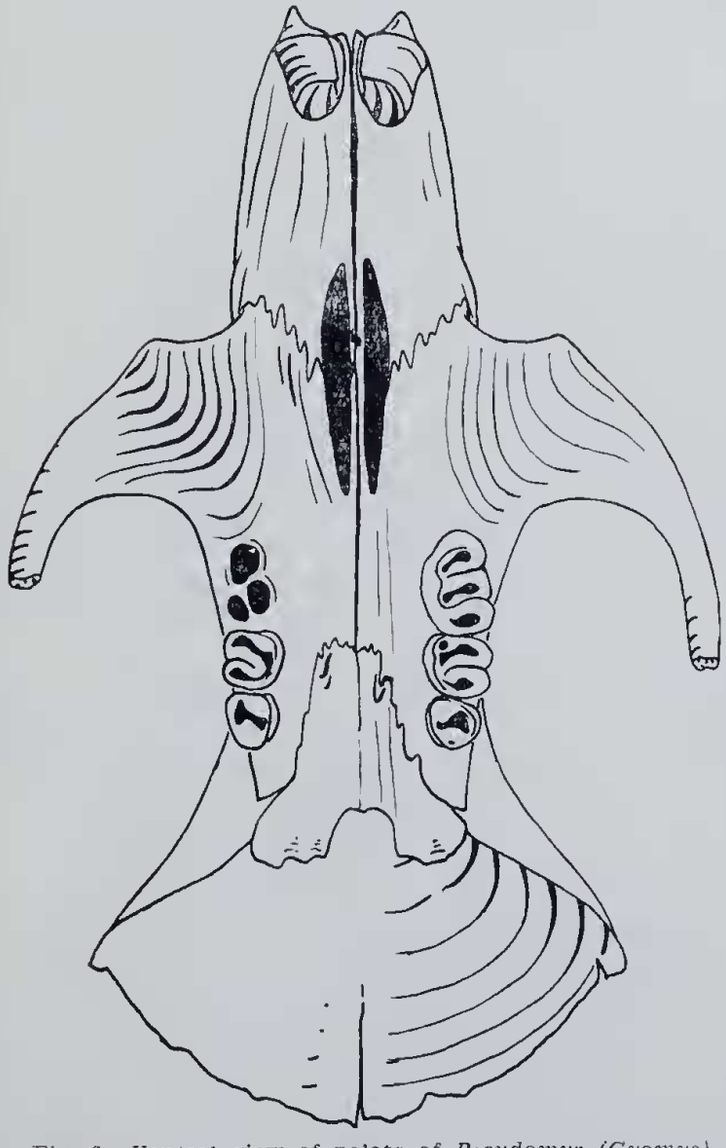

Fig. 6.—Ventral view of palate of *Pseudomys (Gyomys) occidentalis* (CNHM PM4233) from Hasting's Cave. x 5.

Fig. 7.—Lingual view of mandible of *Pseudomys (Gyomys) occidentalis* from Hasting's Cave. x 3.5.

These differences between samples would probably prove to be statistically significant if larger samples were available. The differences are of the kind and degree usually seen between subspecies and probably represent subspecies of *Pseudomys occidentalis*.

Key to the Skulls of Rodents of Southwestern Australia

The identification of skeletal material of rodents is usually considered to be a task for a specialist with access to large collections of comparative material. This is frequently the case and will probably remain so in many instances. It is possible to find in the rodents of southwestern Australia consistent and easily recognized characters which, with few exceptions will allow an identification to species. The key presented here is based on the skull and upper teeth. The identification of the mandibles and lower teeth is very difficult even with access to comparative material.

The geographic area over which this key is expected to apply is western Australia from Geraldton to the south coast and eastward along the Nullarbor Plain to Eucla.

The identification of species of *Rattus* and *Mus* may give trouble. The recognition of the four species of *Rattus* mentioned in the key

should give no trouble but additional species of *Rattus* may have been recently introduced from Asia and will not be identifiable. It is also probable that Asiatic species of *Mus* have been introduced recently. The author has seen specimens trapped in Western Australia which are not referable to any of the species of *Mus* or *Rattus* previously recognized in Western Australia.

A number of species of *Notomys* have been named from Western Australia, four from the western coastal area. Although Mack (1961) has synonomized many of these there is still no reliable way to differentiate the species on the basis of fragmentary material. Consequently this key does not go beyond the gencric lcvel.

Some characters, such as the presence of an accessory cusp on the anterior edge of M^1, the presence of a spine on the zygomatic plate and the number of roots on M^1, which are widely used in the literature should be used with some caution. The accessory cusp on M^1 is supposed to be present in *Pseudomys (Thetomys) nanus*, *Leggadina*, and present or absent in *Notomys* and absent in *Pseudomys (Pseudomys) shortridgei*. *Rattus* is supposed to have five roots on M^1; *Pseudomys*, *Leggadina*, *Notomys* are supposed to have three. The zygomatic plate is supposed to have a spine in *Pseudomys (Thetomys) nanus* and *Notomys*.

In fact, as noted above, a significant percentage of specimens of *Pseudomys (Pseudomys) rawlinnae* and a few specimens of *Pseudomys (Pseudomys) shortridgei* possess the anterior cuspule on M^1. The spine on the zygomatic plate is apparently always present in *Pseudomys (Thetomys) nanus* and *Notomys* and is variable in *Pseudomys (Pseudomys) rawlinnae*. A few specimens of *Pseudomys (Pseudomys) shortridgei* have four or five roots on M^1.

The result of these variations is the virtual impossibility of distinguishing positively *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys) rawlinnae* on the basis of cranial material. For this reason geographic distribution has been used to separate them until satisfactory morphological criteria are found.

A few specimens of *Pseudomys (Pseudomys) shortridgei* which have the anterior accessory cuspule on M^1 are unlikely to be confused with any other species because of size and the lack of a spine on the zygomatic plate. Those with more than three roots on M^1 are easily distinguished from *Rattus* by the poor development of the outer row of cusps on M^{1-2}.

1. M^3_3 absent; M^1_1 greatly enlarged (length greater than 6 mm), wears to form 3 large lakes; root pattern of M^1 complex .... *Hydromys chrysogaster*

   M^3_3 present; M^1_1 not greatly enlarged 2

2. M^1 5-rooted; 3 well developed cusps on 2 anterior lophs of M^1 3

   M^1 3-rooted (or occasionally 4), only 2 well developed cusps on 2 anterior lophs .. 6

3. Snout short; incisive foramina slit-like, occupying a large part of the post incisive diastema and extending well back of the front edge of M^1; interorbital constriction at middle of frontal 4

   Snout long; incisive foramina elliptical with rounded ends, occupying comparatively small part of the post incisive diastema and extending only to anterior edge of M^1; interorbital constriction well anterior to middle of frontal 5

4. Size large, molar row greater than 7 mm ... . *Rattus fuscipes*

   Size medium, molar row less than 7 mm .... *Rattus sp.*

5. Zygomatic plate close to vertical; ridges on sides of braincase parallel .... *Rattus norvegicus*

   Zygomatic plate inclined outward from skull; ridges on side of braincase rounded .... *Rattus rattus*

6. M^1 longer than M^2 plus M^3 notch present on back side of upper incisors .... *Mus musculus*

   M^1 shorter than M^2 plus M^3 notch absent on back side of upper incisors 7

7. Anterior edge of zygomatic plate concavc with anterior projecting spine 8

   Anterior edge of zygomatic plate straight or convex 10

8. Anterior portion of zygomatic arch broadened (2 to 3 times wider than remainder of arch) *Notomys*

   Anterior portion of zygomatic arch not broadened 9

9. Found in Nullarbor Plain .... *Pseudomys (Pseudomys) rawlinnae*

   Found along west coast of Western Australia ... ... *Pseudomys (Thetomys) nanus*

10. Size very small (length M^{1-3} less than 4 mm) 11

    Size medium to large (length M^{1-3} more than 4 mm) 12

11. Accessory cusp on anterior end of M^1 ... . *Leggadina hermannsbergensis*

    Accessory cusp not present on anterior end of M^1 . ... *Pseudomys (Gyomys) albocinereous*

12. Molars small in proportion to size of skull with weak laminae .... *Pseudomys (Gyomys) occidentalis*

    Molars robust with well developed laminae and cusps . . 13

13. Size large (length M^{1-3} more than 6.5 mm) with two rows of heavy cusps on upper molars 14

    Size medium (length M^{1-3} less than 6.5 mm) with two rows of well developed cusps and one of poorly developed cusps on upper molars .... *Pseudomys (Pseudomys) shortridgei*

14. Upper molar row more than 7.5 mm; a small oval foramen immediatcly behind upper incisors; bullae large .... *Leporillus conditor*

    Upper molar row less than 7.5 mm; no small oval foramen immediately behind upper incisors; bullae small .... *Leporillus apicalis*

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